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Detection of Quantitative Trait Loci Influencing Conformation Traits and Calving Ease in Holstein-Friesian Cattle

M. S. Ashwell,[1,4] D. W. Heyen,[2] J. I. Weller,[3] M. Ron,[3] T. S. Sonstegard,[4] C. P. Van Tassell,[4] and H. A. Lewin[2]
[1]Department of Animal Science, North Carolina State University, Raleigh 27695
[2]Department of Animal Sciences, University of Illinois at Urbana-Champaign, Urbana 61801
[3]Institute of Animal Sciences, Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel
[4]Bovine Functional Genomics Laboratory, USDA-ARS, Beltsville, MD 20705

ABSTRACT

An extension of our previous genome scan of a North American Holstein-Friesian population was conducted to identify quantitative trait loci (QTL) affecting conformation traits. Resource families consisted of 1404 sons of 10 elite sires. Genome coverage was estimated to be 2713.5 cM (90%) for 406 markers using a granddaughter design. Regression interval mapping was used to detect QTL affecting 22 conformation traits, including body, udder, feet and legs, and dairy conformation as well as calving ease. Analysis of the families jointly identified 41 chromosome-wise significant QTL influencing conformation traits and 3 significant QTL influencing calving ease on 20 chromosomes. The false discovery rate method was used to account for multiple testing and 3/4 of the suggestive and 5/6 of significant QTL should be real effects. Fourteen of the 44 QTL were significant at the genome-wise level. Comparison of these results with other published reports identifies common QTL affecting conformation traits. Regions on 10 chromosomes appear to affect multiple traits, including conformation, milk production, and somatic cell score, within these particular US Holstein families. Additional work is needed to determine the precise locations of the QTL and select positional candidate genes influencing these traits.
(**Key words:** genome scan, dairy, conformation, quantitative trait loci)

Abbreviation key: BD = body depth, **BTA** = *Bos taurus* chromosome, **DBDR** = Dairy Bull DNA Repository, **FA** = foot angle, **FTP** = front teat placement, **FUA** = fore udder attachment; **RA** = rump angle, **RUH** = rear udder height, **TL** = teat length, **UD** = udder depth.

INTRODUCTION

During the last 10 yr, numerous studies from around the world have concentrated on identifying QTL affecting economically important traits in various breeds of dairy cattle. Although the experimental designs, analysis methods, and significance thresholds have varied from study to study, several common QTL affecting milk production traits were detected (Georges et al., 1995; Ron et al., 1998, 2004; Zhang et al., 1998; Heyen et al., 1999; Ashwell et al., 2001; Klungland et al., 2001; Nadesalingam et al., 2001; Boichard et al., 2003). Many fine-mapping studies have commenced (Arranz et al., 1998; Kühn et al., 1999; Ron et al., 2001), and recently, candidate genes underlying 2 of these QTL have been identified (Grisart et al., 2002; Blott et al., 2003). How these discoveries will impact future dairy production has yet to be determined.

Recent studies have focused on detection of QTL affecting conformation and functional traits (Spelman et al., 1999; Schrooten et al., 2000; Boichard et al., 2003; Hiendleder et al., 2003). Although the benefits of identifying QTL for conformation traits are less obvious, significant genetic correlations between them and production and health traits have been found. Examples include stature and production (Short and Lawlor, 1992), feet and leg scores and longevity (Klassen et al., 1992; Dekkers et al., 1994; Vollema and Groen, 1996), conformation and calving interval (Dadati et al., 1986), udder type and SCS (Rogers and Hargrove, 1993; Rogers et al., 1991, 1995), and dairy form and metabolic disease (Rogers et al., 1999). Indeed, most breeding programs include nonproduction traits because of these genetic correlations or because they have a direct impact on the animal's merit. Several of the linear conformation traits such as dairy form, foot angle, and udder depth are useful predictors of an animal's lifetime net merit and longevity in the herd (Vollema et al., 2000). Therefore, detection of QTL affecting these traits may lead to selection for improved conformation and improve-

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Corresponding author: Melissa Ashwell; e-mail: Melissa_Ashwell@ncsu.edu.

Table 1. Number of sons genotyped and those that have conformation and calving ease trait records in each grandsire family.

Family	Genotyped	Conformation traits[1]	Feet and leg score	Calving ease
1	241	228	149	237
2	223	222	222	223
3	178	160	54	178
4	150	141	30	150
5	150	131	84	147
6	113	113	110	113
7	86	84	72	86
8	101	77	46	98
9	92	87	59	92
12	70	59	15	69
Total	1404	1302	841	1393

[1]Excluding feet and leg score.

ment for traits such as production, longevity, mastitis resistance, and reproduction.

The results presented herein represent the second phase of a genome scan of a US Holstein population for QTL influencing production, health, reproduction, and conformation traits. Results of a scan for QTL affecting production traits, SCS, and daughter pregnancy rate were previously reported (Ashwell et al., 2004). Putative QTL exceeding chromosome-wise suggestive and significant thresholds for conformation traits and calving ease are presented.

MATERIALS AND METHODS

Resource Populations and Description of Phenotypic Data

Ten large half-sib families from the Dairy Bull DNA Repository (**DBDR**; Da et al., 1994) consisting of 1414 bulls were selected for QTL detection using the granddaughter design. The DBDR family sizes ranged from 70 to 241 progeny-tested sons that were genotyped, but family size was generally smaller due to missing conformation phenotypes (Table 1). The Holstein Association, USA (1999) provided the conformation trait data (May 2003 release) and the Animal Improvement Programs Laboratory of USDA-ARS provided the calving ease data (February 2002 release). Four groups of type traits with available composite indexes were used: udder, body form, feet and legs, and dairy capacity. The individual traits for each composite index are as follows: the udder group, consisting of fore udder attachment (**FUA**), rear udder height (**RUH**), rear udder width, udder depth (**UD**), udder cleft, front teat placement (**FTP**), and teat length (**TL**); the body form group, consisting of stature, body depth (**BD**), rump angle (**RA**), and thurl width; the feet and legs group, consisting of feet and leg score, rear legs-side view, rear legs-rear view, and foot angle (**FA**); and the dairy capacity group, consisting of dairy form and strength. The standardized PTA for the 17 linear conformation traits and composite indices and the PTA for an overall type composite and direct maternal effects for calving ease (percent difficult births) were analyzed.

Genotyping

Genotyping methods and genome coverage for the 406 typed markers are summarized in Ashwell et al. (2004). Briefly, microsatellite markers were selected at approximately 20-cM intervals from published bovine maps (Barendse et al., 1994, 1997; Bishop et al., 1994; Ma et al., 1996; Kappes et al., 1997). Genome coverage was estimated to be 2713.5 cM (90%), assuming a 3000-cM genome. The average marker interval was 7.4 cM.

Statistical Methods

Similar to the analysis procedures in Ashwell et al. (2004), data were analyzed using a regression approach described by Haley and Knott (1992). The web-based version of the method (QTL Express; Seaton et al., 2002; http://qtl.cap.ed.ac.uk) was used to detect QTL within and across the families. Analysis was conducted at 1-cM intervals along each chromosome. The reliability of each bull's standardized PTA was used as the weight variable in the analysis to give increased value to bulls with higher accuracies. Bootstrapping using 1000 resamples was used to calculate the 95% QTL position confidence intervals. Chromosome-wise significance thresholds were calculated from the *F*-statistics using permutation testing as described by Churchill and Doerge (1994). One thousand permutations were completed to determine the critical threshold values. Chromosome-wise thresholds were calculated for all chromosome-trait combinations (Table 2). Suggestive ($P < 0.05$) and significant ($P < 0.01$) chromosome-wise *F*-value thresholds for the different traits were used to identify putative QTL and are summarized in Table 2.

The QTL Express method will calculate genome-wise threshold values using permutation testing, but is limited to a total of 345 individuals on 29 chromosomes (total must be ≤10,000). Therefore, an alternative method based on Spelman et al. (1999) was used to determine which QTL were significant at the genome-wise level. In this calculation, *F*-statistics generated by QTL Express were converted to *P*-values using the SAS PROBF function (SAS Institute, 2005). The genome-wise *P*-value (P_{genome}) for each chromosome-wise significant QTL was calculated using $P_{genome} = 1 - (1 - P_{chr})^n$, where P_{chr} is the chromosome-wise *P*-value and n is the total number of chromosomes (n = 29).

To account for multiple testing, due to both multiple traits and markers, the false discovery rate (Benjamini

Table 2. Range of chromosome-wise permutation thresholds calculated for each trait on all 29 autosomes.

Trait	Average suggestive threshold ($P < 0.05$)	Suggestive threshold range	Average significant threshold ($P < 0.01$)	Significant threshold range
Body depth	2.40	2.22–2.59	2.98	2.65–3.25
Body form composite index	2.43	2.19–2.63	3.00	2.63–3.23
CE_PDB[1]	2.32	2.15–2.43	2.87	2.71–3.10
Dairy form	2.39	2.13–2.57	2.98	2.63–3.27
Dairy capacity composite index	2.30	2.12–2.42	2.86	2.65–3.07
Foot angle	2.53	2.34–2.73	3.20	2.91–3.43
Feet and legs composite index	2.54	2.34–2.83	3.16	2.87–3.57
Feet and legs score	2.47	2.34–2.62	3.03	2.80–3.29
Front teat placement	2.50	2.25–2.71	3.11	2.79–3.36
Fore udder attachment	2.55	2.35–2.78	3.13	2.94–3.46
PTA for type	2.42	2.23–2.57	3.00	2.59–3.25
Rump angle	2.32	2.07–2.44	2.82	2.59–2.99
Rear legs-rear view	2.53	2.35–2.73	3.15	2.87–3.45
Rear legs-side view	2.47	2.31–2.66	3.12	2.80–3.56
Rear udder height	2.62	2.47–2.87	3.22	2.96–3.49
Rear udder width	2.49	2.33–2.67	3.05	2.76–3.34
Stature	2.40	2.19–2.55	2.94	2.70–3.11
Strength	2.49	2.25–2.68	3.05	2.87–3.38
Teat length	2.39	2.22–2.53	2.94	2.72–3.25
Thurl width	2.38	2.17–2.53	2.89	2.72–3.10
Udder cleft	2.51	2.31–2.64	3.08	2.84–3.27
Udder depth	2.30	2.12–2.53	2.82	2.59–3.04
Udder composite index	2.48	2.27–2.66	3.02	2.83–3.19

[1]CE_PDB = Calving ease, percent difficult births.

and Hochberg, 1995; Weller et al., 1998) was applied. Twenty-three traits were evaluated on 29 chromosomes, a total of 667 tests.

Within-family analysis was conducted for QTL identified in the across-family analysis to determine which DBDR families appeared to be segregating for the QTL. Suggestive thresholds ($P < 0.05$) were calculated using 1000 permutations for all trait-family-chromosome combinations (data not shown).

RESULTS

Conformation Traits

Analysis of all families jointly identified 41 chromosome-wise significant QTL influencing 18 conformation traits on 17 chromosomes (Table 3). Fourteen of these QTL were significant at the genome-wise level. Eighty-one QTL were detected at the suggestive level influencing all 22 conformation traits on all *Bos taurus* autosomes (**BTA**) except BTA8, BTA11, and BTA21. Within-family analysis was conducted to identify which DBDR families appear to be segregating for the QTL (Table 3). Two QTL, on BTA13 for PTA for type and BTA14 for RA, did not have at least one family reach the suggestive *F*-value threshold. Several families approached their specific suggestive thresholds; this may explain why QTL were identified when the families were analyzed jointly.

Calving Ease

Three significant and 3 suggestive QTL affecting calving ease were detected in the joint family analysis (Table 3) located on 6 chromosomes. At least one DBDR family exceeded the suggestive level for each of these QTL when the families were analyzed individually.

False Discovery Rates

At the 0.05 and 0.01 type I error levels, 33.35 and 6.67 tests, respectively, are expected to be significant by chance alone. False discovery rates were calculated to account for this multiple testing. At the 5% type I error level, the false discovery rate is 33.35/128 (total number of suggestive QTL), or 26.1%. At the 1% error level, the false discovery rate is 6.67/41, or 16.3%. Therefore, 3/4 of the suggestive and 5/6 of significant QTL should be real effects.

DISCUSSION

A genome scan identified significant QTL influencing conformation and calving ease traits in this North American Holstein-Friesian cattle population. A total of 128 putative QTL significant at various stringencies were identified in this study. Fourteen of these QTL were significant at the genome-wise level, affecting body and udder traits, with no genome-wise significant

Table 3. Suggestive and significant effects on calving ease and conformation traits.

BTA	Trait[1]	QTL location (cM)	*F*-statistic[2]	Marker interval	95% CI (cM)	Families above suggestive level
1	**FTP**	**119**	**3.33**	**BM1824–BMS599**	**20-140**	**3, 9**
1	UC	119	2.73	BM1824–BMS599	0-140	6
2	**BD**	**21**	**3.1**	**TGLA431–TGLA377**	**0-74**	**12**
2	**BI**	**21**	**3.37**	**TGLA431–TGLA377**	**0-69**	**3**
2	FUA	2	2.88	BM3627–TGLA44	0-91	4
2	PTAT	0	2.6	Centro–TGLA44	0-92	4
2	**STA**	**24**	**3.31***	**TGLA377–URB042**	**0-67.5**	**3**
2	STR	3	3.07	TGLA44–TGLA431	0-92	3
2	TW	2	2.47	BM3627–TGLA44	0-74	3, 4
3	FA	65	3.15	BM4301–HUJI177	9-97	4, 5, 6
4	BD	4	2.54	BMC1410–RM188	0-128	3, 8
4	STA	28	2.48	BMS1634–MAF70	0-128	8
5	DF	46	2.79	AGLA293–BL37	2-119	5
5	**FTP**	**119**	**3.67***	**BM43–URB060**	**51-119**	**2, 7**
5	**FUA**	**112**	**3.56***	**BM315–BM2830**	**52-119**	**2, 7**
5	**PTAT**	**109**	**3.39***	**BM315–BM2830**	**60-119**	**2, 7**
5	**RA**	**112**	**2.96**	**BM315–BM2830**	**59-119**	**2**
5	RUH	118	2.7	BM43–URB060	23-119	2
5	**TL**	**43**	**3.04**	**AGLA293–BL37**	**0-111.5**	**2, 4, 5**
5	**UI**	**119**	**3.09**	**BM43–URB060**	**51-119**	**2, 7**
6	FA	67	2.94	BM4322–BMS470	0-119.5	1
6	FTP	0	2.9	Centro–ILSTS093	0-86	3
6	TL	133	3.16	BMS5021–BMC4203	40.5–133	1, 6, 8
7	BD	95	2.57	BB719–BM9065	0-111	1
7	**FA**	**83**	**2.94**	**BB719–BM9065**	**12-100**	**1, 5**
7	UC	8	2.71	TGLA48–BP41	0-117	8
8	**CE_PDB**	**116**	**3.08**	**BMS2847–BMS2629**	**0-116**	**1, 8**
9	CE_PDB	96	2.4	BM4208–BMS1943	0-96	8, 12
9	**RA**	**58**	**3.06**	**BMC701–BMS1290**	**7-93**	**1, 2, 8**
9	RLSV	61	2.63	URB024–TGLA73	0-96	8
9	STR	64	2.62	URB024–TGLA73	7-87	2, 12
10	**BD**	**46**	**3.06**	**BL1035–BM875**	**29-111**	**8, 12**
10	FUA	116	2.71	BMS2614–CSRM60	0-116	1
10	STR	42	2.83	BL1035–BM875	5.5–112	3, 9
12	**FLI**	**41**	**3.08**	**BM6404–BMS975**	**0-83**	**1**
12	FLS	42	2.48	BM6404–BMS975	0-83	1
12	RLRV	41	2.95	BM6404–BMS975	0-83	1, 6, 7
13	DF	0	2.82	Centro–TGLA23	0-84	3, 4, 12
13	FA	54	2.71	UWCA25–BL42	20-83	4, 7, 8
13	**FUA**	**63**	**3.24**	**BMS1226–BMS995**	**0-81.5**	**3, 7**
13	PTAT	62	2.76	BMS1226–BMS995	18.5–74.5	
13	**RUH**	**66**	**3.53**	**BMS1226–BMS995**	**0-76**	**2, 8**
13	**RUW**	**63**	3.14	**BMS1226–BMS995**	**0-73**	**2**
13	UD	72	2.44	BMS1226–BMS995	0-84	3, 7
13	**UI**	**64**	**3.61***	**BMS1226–BMS995**	**0-84**	**2, 3, 7**
14	FA	54	2.73	BMS1899–BM4513	0-76	8
14	FTP	48	2.7	BMS740–BMS1899	1-84	12
14	RA	33	2.41	BMS1941–BM8215	0-85	
14	**UC**	**51**	**3.15**	**BMS740–BMS1899**	**0.5–85**	**1, 3, 4**
15	BI	45	2.88	HBB–ILSTS061	12.5–75	1, 3
15	**FTP**	**52**	**3.22**	**HBB–ILSTS061**	**0-91.5**	**3, 6**
15	**FUA**	**36**	**4.16***	**BMS2684–HBB**	**0-55**	**3, 4, 5**
15	**PTAT**	**47**	**4.01***	**HBB–ILSTS061**	**0-74**	**3, 4**
15	**STA**	**37**	**3.23**	**BMS2684–HBB**	**14-80**	**1, 3**
15	TW	48	2.51	HBB–ILSTS061	14-80	1, 3
15	**UC**	**55**	**3.16**	**HBB–ILSTS061**	**0-87.5**	**3, 5, 8**
15	**UD**	**37**	**3.51***	**BMS2684–HBB**	**5-92**	**4, 5, 9**
15	**UI**	**45**	**4.44***	**HBB–ILSTS061**	**0-64**	**1, 3, 4, 5**
16	**BD**	**1**	**3.56***	**Centro–BM6430**	**0-93**	**2, 4, 8**
16	BI	0	3.1	Centro–BM6430	0-93	2, 4
16	PTAT	1	2.5	MGTG1–TGLA245	0-93	9
16	**RLRV**	**0**	**3.24**	**Centro–BM6430**	**0-93**	**6, 9, 12**
16	**STR**	**0**	**3.59***	**Centro–BM6430**	**0-93**	**2, 4, 9**
16	TL	48	2.65	TGLA53–IDVGA49	0-81.5	2, 4, 9
16	TW	0	2.7	Centro–BM6430	0-93	4, 9
16	**UD**	**61**	**3.28**	**BB709–INRA048**	**15.5–84.5**	**8, 12**
17	**CE_PDB**	**69**	**3.19**	**BM305–URB002**	**0-86**	**3, 4, 7, 8**
17	RUH	69	2.61	BM305–URB002	4-97.5	3

Continued

Table 3 (Continued). Suggestive and significant effects on calving ease and conformation traits.

BTA	Trait[1]	QTL location (cM)	*F*-statistic[2]	Marker interval	95% CI (cM)	Families above suggestive level
17	TL	78	2.47	BM8125–BM1862	2-91.5	1, 4, 5, 6
18	FUA	33	2.67	BMS2213–BM7109	16-67	5
18	**RUH**	**28**	**3.87***	**BMS2213–BM7109**	**16-64**	**5, 7**
18	**UD**	**36**	**2.88**	**BMS2213–BM7109**	**0-78**	**3, 5**
18	UI	29	2.81	BMS2213–BM7109	13.5–77	3
19	STA	0	2.54	Centro–BM6000	0-96.5	8, 9
19	TL	76	2.58	CSSM65–IDVGA44	2.5–95	8
20	BD	36	2.69	BM713–BMS2361	0-64	3, 7, 12
20	BI	38	2.58	BM713–BMS2361	0-64	3, 12
20	DI	30	2.35	RM310–TGLA126	0-51	3, 7
20	FUA	66	2.62	BM5004–AFR2215	2-69	2, 3
20	RA	8	2.94	BM1225–RM310	0-46.5	8, 9
20	**STR**	**38**	**3.17**	**BM713–BMS2361**	**0-65**	**2, 3, 12**
20	**TW**	**38**	**3.98***	**BM713–BMS2361**	**0-64**	**2, 4, 7, 12**
22	RA	60	2.6	CSSM41–BMS875	0-81	2
22	STA	72	2.43	BMS875–BM4102	0-81	2
22	**UC**	**0**	**3.13**	**Centro–CSSM26**	**0-81**	**6, 7**
22	UI	0	2.78	Centro–CSSM26	0-74	2, 6
23	BD	0	2.73	Centro–INRA132	0-67	3
23	BI	0	2.86	Centro–INRA132	0-67	3
23	CE_PDB	62	2.86	CSSM24–BM1905	0-67	3, 5
23	DI	0	2.48	Centro–CSSM5	0-40.5	8
23	FTP	24	2.9	BM1258–MGTG7	0-67	4, 5
23	FUA	16	3.15	CSSM5–BM1258	0-62	1, 6
23	STA	0	2.66	Centro–CSSM5	0-67	3
23	UD	49	2.45	BB705–BM1818	0-67	1
23	UI	17	2.76	CSSM5–BM1258	0-67	1
24	BD	11	2.45	BM7151–AGLA269	1-52	8
24	BI	14	2.44	BM7151–AGLA269	1-52	8
24	CE_PDB	22	2.45	BM7151–AGLA269	0-56	5
24	FUA	48	2.82	BMS1332–URB031	8-56	6, 7, 12
24	STR	16	2.44	BM7151–AGLA269	1.5–52	8
24	UD	56	2.5	URB031–BMS3024	6-56	7, 12
24	UI	51	2.5	BMS1332–URB031	1-56	6, 7
25	FA	39	2.4	BMS1353–BM1864	0-46	1
25	FLI	7	2.51	BM4005–URB036	0-44	1
26	BI	0	2.53	Centro–BM4505	0-66	3
26	FTP	42	2.62	BM804–ARO25	0-66	3, 5
26	TL	31	2.46	BM6041–BM804	0-66	5, 6
26	**UD**	**66**	**2.9**	**BM804–ARO25**	**0-66**	**3**
26	UI	66	2.77	BM804–ARO25	0-66	3
27	**CE_PDB**	**36**	**2.97**	**BMS689–CSSM36**	**1-64**	**12**
27	DF	32	2.63	BMS1385–CSSM43	0-65	2, 8
27	STA	6	2.51	TGLA179–BM871	0-65	3, 6, 8
28	FA	48	2.43	BM6466–BM2515	0-48	9
28	FLI	48	2.64	BM6466–BM2515	0-48	9
28	FUA	8	2.92	BP23–BL25	1-48	5
28	RLRV	26	2.68	BL25–BM6466	0-48	5, 9
28	RUH	25	2.77	BL25–BM6466	1-48	5
28	RUW	16	2.7	BP23–BL25	2-48	5, 12
28	**UI**	**26**	**2.94**	**BL25–BM6466**	**2-48**	**5, 12**
29	FA	34	2.46	BMS3224–BMC6004	0-50	7, 8
29	FLI	34	2.79	BMS3224–BMC6004	7-49	8
29	FLS	32	2.71	BMS1600–BMC3224	7-48	8
29	**FTP**	**21**	**2.94**	**BMS1600–BMC3224**	**8.5–36.5**	**3**
29	**FUA**	**23**	**3.18**	**BMS1600–BMC3224**	**1-49**	**2, 3, 12**
29	**PTAT**	**22**	**3.98***	**BMS1600–BMC3224**	**8.5–36.5**	**3, 8, 12**
29	RUH	16	2.65	BMC8012–BMS1600	0-51	1, 2, 3
29	RUW	13	2.53	BMC8012–BMS1600	0-49	1, 5
29	**UI**	**22**	**3.24**	**BMS1600–BMC3224**	**7.5–49**	**2, 3**

[1]Traits: FTP = front teat placement; UC = udder cleft; BD = body depth; BI = body form composite index; FUA = front udder attachment; PTAT = PTA for type; STA = stature; STR = strength; TW = thurl width; FA = foot angle; DF = dairy form; RA = rump angle; RUH = rear udder height; TL = teat length; UI = udder composite index; CE_PDB = calving ease, percent difficult births; RLSV = rear legs-side view; FLI = feet and legs composite index; FLS = feet and legs score; RLRV = rear legs-rear view; RUW = rear udder width; DI = dairy capacity composite index; UD = udder depth.

[2]Chromosome-wise suggestive QTL in normal font; chromosome-wise significant QTL in boldface, and genome-wise significant QTL marked by *.

QTL identified for any feet and leg traits. Forty-four QTL significant at the chromosome-wise level were identified on 20 of the 29 autosomes. The majority of these significant QTL affected body and udder traits, with only 3 QTL affecting feet and leg traits. This was not surprising due to the large number of animals that were missing feet and leg evaluations (Table 1), but may also suggest that there are fewer QTL with large effects affecting feet and leg traits, at least in these 10 families. At least 1 suggestive QTL was detected for all traits, ranging from 1 QTL affecting rear leg-side view to 7 QTL affecting FUA.

Ashwell et al. (2004) identified putative QTL affecting milk production, SCS, productive life, and daughter pregnancy rate using the same set of genotypic data. When the families were analyzed jointly, QTL affecting milk production and composition traits were identified on BTA3, BTA6, BTA7, BTA11, BTA14, and BTA20 (Ashwell et al., 2004). Quantitative trait loci affecting SCS were identified on BTA7, BTA22, BTA23, and BTA26 (Ashwell et al., 2004). In the current report, QTL affecting udder cleft, BD, and FA were identified on BTA7 in the same region of the chromosome (Table 3). This suggests the possibility of one QTL having pleiotropic effects; however, the 95% confidence intervals calculated using bootstrapping methods are quite large, making multiple QTL affecting these disparate traits a more likely scenario. Quantitative trait loci affecting several conformation traits were identified on BTA14 and BTA20. *Bos taurus* autosome 14 carries the acyl CoA:acylglycerol acyltransferase 1 gene that has been shown to have major effects on milk fat yield (Grisart et al., 2002). Other studies have reported evidence of additional QTL affecting milk production traits on this chromosome (Heyen et al., 1999; Mosig et al., 2001). Quantitative trait loci affecting milk yield, milk protein percentage, SCS (Ashwell et al., 2004), and body traits (Table 3) were detected on BTA20. This chromosome carries the growth hormone receptor gene that was reported to have a phenylalanine-to-tyrosine polymorphism that is strongly associated with effects on milk yield, milk protein percentage, and milk fat percentage (Blott et al., 2003). This gene mapped to approximately 43 cM on their linkage map and is located in the same region as the QTL affecting thurl width, body depth, and strength (36 to 38 cM) in this study. Therefore, it is possible that variation in the growth hormone receptor gene affects animal conformation traits as well as milk production and milk composition traits; however, we have not genotyped these animals at the growth hormone receptor polymorphism reported by Blott and coworkers (2003).

Chromosomes reported to contain SCS QTL (Ashwell et al., 2004) also appear to carry QTL affecting conformation traits (Table 3). Chromosomes 22 and 26 provide evidence of QTL affecting SCS and udder and body traits in the same regions of the chromosomes (Table 3). Somatic cell score is highly correlated with mastitis incidence and moderately correlated with udder type traits (Shook and Schutz, 1994). Correlations between linear type traits and SCS are –0.28 for UD, –0.21 for FTP, and –0.16 for udder cleft (Schutz et al., 1993). Subsequently, selection of individuals with higher udders, stronger fore udder attachments, closer teat placement, and shorter teats should decrease mastitis incidence by reducing injury frequency and exposure to bacteria (Rogers et al., 1991; Rogers and Hargrove, 1993). Mastitis costs the dairy industry approximately $2 billion each year in lost production and health expenses (Harmon, 1994). Reduction of these costs may be realized through marker-assisted selection programs, but much work still needs to be done at the molecular level to fine-map the QTL and identify candidate genes. The number of candidate genes associated with QTL affecting SCS may be reduced on the basis of genetic correlations between udder type and SCS. Presently, 2 biological mechanisms of mastitis resistance exist, immunological and structural (i.e., udder attachment, front teat placement, teat length, and teat shape). Quantitative trait loci on BTA22 and BTA26 affect SCS and udder type, suggesting that the effects on these chromosomes may be related to udder structure, and not immune function.

Quantitative trait loci affecting SCS and body and udder traits have also been detected on BTA23, which carries the major histocompatibility complex. This complex has been mapped to approximately 41 cM on the linkage map (http://www.marc.usda.gov) and is included in the 95% confidence interval for the conformation QTL (Table 3). Therefore, it is likely that this chromosome carries genes affecting body and udder conformation in addition to the genes affecting immune response; however, 1 QTL having pleiotropic effects cannot be ruled out due to the large confidence intervals.

Previous investigators have reported QTL influencing conformation traits in different populations (Spelman et al., 1999; Schrooten et al., 2000; Boichard et al., 2003; Hiendleder et al., 2003). Spelman et al. (1999) identified a QTL for stature with suggestive linkage on BTA14 situated at 36 cM on the linkage map. We did not detect a QTL affecting stature but did detect QTL affecting FTP, FA, and RA (Table 3) on this chromosome.

Schrooten et al. (2000) identified a number of QTL with either genome-wise or chromosome-wise significance. They reported QTL affecting conformation and functional traits on 22 chromosomes. Comparison be-

tween their findings and those reported here identify 6 chromosomes with similar QTL. Both studies identified effects on body traits on BTA2. Schrooten et al. (2000) identified effects on chest width, body capacity, and rump width, whereas the present study identified effects on strength, BD, and stature (Table 3). Positions of the putative QTL vary between the 2 studies with Schrooten et al. (2000) placing the QTL at the telomeric end and the current study placing the QTL at the centromeric end (Table 3). Therefore, the 2 studies provide evidence that at least 1, and maybe 2, QTL influence body traits on BTA2.

Quantitative trait loci affecting udder and body traits were identified on BTA5 in both studies. Schrooten et al. (2000) identified QTL affecting body capacity, size, rump width, and dairy character, whereas we identified QTL affecting dairy form and RA (Table 3). Effects on udder traits were consistent across both studies, and the confidence intervals calculated here easily overlap the regions reported by Schrooten et al. (2000). Therefore, this report provides additional evidence of a QTL or several closely linked QTL influencing udder and body traits existing on BTA5.

Bos taurus autosome 6 provided evidence of QTL affecting feet and legs traits in both studies. Schrooten et al. (2000) reported a rear leg set QTL at 85 cM, and the present study places a QTL affecting FA at 67 cM (Table 3).

The remaining significant effects identified in the study published by Schrooten et al. (2000) were not detected in the present study except for QTL affecting udder traits on BTA10, BTA13, BTA23, and BTA26. On BTA10, Schrooten et al. (2000) reported QTL affecting FUA and FTP, whereas the present study identified QTL affecting FUA (Table 3). On BTA13, Schrooten et al. (2000) identified QTL affecting FUA and UD, and here, QTL affecting UD, FUA, rear udder width, RUH, and udder composite index were reported (Table 3). On BTA23, both studies identified QTL affecting FUA at the same approximate location. On BTA26, they reported a QTL affecting FUA and udder, and the present study identified QTL affecting FTP, TL, UD, and udder composite index (Table 3) on the same chromosome.

More recently, Schrooten et al. (2004) used their data set to detect chromosomal regions affecting multiple traits by computing the covariance between contrasts for milk production, udder, SCS, and fertility traits. Comparison of their results and those presented here is difficult because most of the trait combinations reported by Schrooten and coworkers (2004) involved a contrast of 1 udder trait to 1 production trait. When examining only those chromosomal regions affecting 2 udder traits, they identified putative QTL on BTA6, BTA19, BTA20, BTA23, and BTA25. Results presented here identified suggestive QTL affecting udder traits on BTA6, BTA19, BTA20, and BTA23. On BTA6, Schrooten et al. (2004) detected a significant chromosomal region when contrasting FUA and FTP, which had not been identified when the traits were analyzed separately. A QTL affecting FTP was identified in the US Holstein population (Table 3). On BTA19, Schrooten et al. (2004) detected a significant chromosomal region affecting udder traits when contrasting UD and FUA, RUH and FUA, and RUH and FTP. In this study, a suggestive QTL affecting a different udder trait, TL, is reported (Table 3). On BTA20, Schrooten et al. (2004) detected a chromosomal region when contrasting UD and FUA and, in our study, a suggestive QTL affecting FUA is reported. On BTA23, Schrooten et al. (2004) detected a significant chromosomal region when contrasting UD and FTP and then FUA and FTP. Using the DBDR families, QTL affecting FUA, FTP, and UD were placed at 16, 24, and 49 cM, respectively (Table 3).

Hiendleder et al. (2003) identified 60 QTL affecting conformation and behavior in German Holsteins. The effects detected in their study were not found in our study with the exception of effects on BTA5 and BTA6. As discussed previously, QTL affecting udder traits were detected in the present study on BTA5 and also detected in the study conducted by Hiendleder and coworkers (2003). On BTA6, the present study detected QTL affecting FA whereas Hiendleder et al. (2003) reported QTL affecting FA and the quality of the feet and legs in the same region on the chromosome.

Boichard et al. (2003) detected QTL affecting milk production, conformation, fertility, and disease resistance in 3 French dairy cattle breeds. They identified 120 QTL that were significant at the chromosome-wise level; 32 of which were significant at the genome-wise level. Comparison of their QTL to those identified in the present study is difficult due to the differences in the number of traits, trait names, and definitions between the 2 countries. For example, the French study evaluated rump length but data on this trait are not routinely collected in the US. Therefore, only 9 QTL appear to have been detected in both studies: on BTA2 affecting BD (US)/chest depth (French) and stature (US)/height at sacrum (French); BTA6 affecting TL and FTP; BTA7 affecting FA (US)/heel depth (French); BTA13 affecting UD; BTA20 affecting BD (US)/chest depth (French) and thurl width (US)/rump width (French); and BTA24 affecting BD (US)/chest depth (French). *Bos taurus* autosome 8 may also harbor QTL that are common across the 2 studies, detected as a calving ease (% difficult births) QTL in the US population and a rump width QTL in the 3 French breeds. The remaining QTL unique to each of these studies may be explained by differences in analysis methods, significance threshold levels, ge-

nome coverage, breed, and specific families that were selected for each study.

The importance of conformation traits for longevity and disease resistance will likely increase as the dairy industry employs confinement-type production practices. Results from this study provide additional evidence that QTL affecting conformation traits exist and could be used in marker-assisted selection programs to eliminate animals that are predisposed to disease and injury. However, additional work is needed to determine the precise locations of these QTL before they can be used for marker-assisted selection because the QTL location confidence intervals are extremely large. The 95% confidence intervals ranged from 28 to 140 cM, with an average of 73.7 cM. Large confidence intervals are expected when using a granddaughter design due to the limited number of genotyped animals and informative families. This project is being continued through addition of new families and expansion of existing families to increase the number of informative meioses so several of the QTL identified in the DBDR families can be fine-mapped and used in marker-assisted selection programs.

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